BIOLOGICAL HISTORY AND AGE ESTIMATION FROM THE ZONES, CHECKS, AND MICROINCREMENTS OF THE OTOLITH OF THE ALFONSIN, *BERYX SPLENDENS* (BERYCIDAE)

by

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ABSTRACT. - Whole otoliths of *Beryx splendens* showed multiple opaque and hyaline zones when observed by transmitted light. SEM studies of whole otoliths showed regular surface sculpturing with widths similar to the widths observed between opaque zones. Optical and etched (SEM) sections of otoliths showed a continuous series of microincrements from the nucleus to the edge of the otolith along the longest prism of the otolith from the nucleus to the dorsal edge axis. Microincrements typically progressed from wide microincrements near the nucleus to narrow microincrements towards the edge of the otolith. A general length-at-age curve was generated by plotting microincrement width against the length of the prism. Growth curves based on microincrement widths indicated similar growth rates (over equivalent size ranges) to those derived from previously published tagging studies. Microincrement growth patterns in the otolith show periodic changes in optical density (and etch-sensitivity) that are generally equivalent to the checks observed in otoliths of other species. Checks caused by cessation of growth could be distinguished from local perturbations in microincrement deposition, and their effect on age estimation errors could be assessed. Microincrement width-based growth curves showed high and variable growth rates in younger fishes, and lower and less variable growth rates in older fishes. Growth curves based on ages estimated from average microincrement widths were compared with growth curves based on other ageing techniques, and the length-at-age distribution patterns based on different growth curves were compared.

RÉSUMÉ. - En lumière transmise, les otolithes de *Beryx splendens* présentent de multiples zones opaques et hyalines. L'examen au MEB montre une surface régulièrement ornementée de bandes semblables à celles qui sont situées entre des zones opaques. Des coupes observées en lumière transmise ainsi qu'au MEB montrent une série continue de microstries de croissance depuis le nucleus jusqu'au bord de l'otolithe alignées selon le plus long prisme de l'otolithe développé depuis le nucleus jusqu'à l'axe de la bordure dorsale. Les microaccroissements sont typiquement larges près du nucleus et étroits au niveau de la bordure de l'otolithe. Une courbe générale longueur/âge est tracée à partir des relations largeurs des microaccroissements/longueur du prisme. Des courbes de croissance fondées sur les largeurs des microaccroissements indiquent des taux de croissance similaires (pour un échantillonnage de taille équivalent) à ceux qui ont été décrits dans des études de marquages déjà publiées. Les patrons de croissance des microaccroissements dans les otolithes présentent des changements périodiques de densité optique (et de sensibilité à l'acide) qui sont, en général, équivalents aux marques d'arrêts de croissance observées dans les otolithes d'autres espèces. Ces marques, provoquées par des arrêts de croissance, pourraient être différentes de celles qui sont provoquées par des perturbations locales dans le dépôt des microaccroissements et leurs effets sur l'estimation de l'âge pourraient être évalués. Des courbes de croissance fondées sur la largeur des microaccroissements montrent des taux de croissance élevés et variables chez les jeunes poissons, alors qu'ils sont plus faibles et moins variables chez les poissons âgés. Les courbes de croissance fondées sur des âges estimés à partir de la largeur moyenne des microaccroissements ont été comparées à d'autres courbes fondées sur d'autres techniques d'estimation de

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l'âge, et les patrons de distribution âge/longueur fondés sur différents courbes de croissances ont été comparés.

Key-words. - Berycidae, *Beryx splendens*, Otoliths, Checks, Microincrements, Age.

The alfonsin, *Beryx splendens* (Beryciformes) competes well enough with other fish species to be sufficiently abundant to be fished commercially in Japan (Ikenouye and Masuzawa, 1967; Ikenouye, 1969; Masuzawa *et al.*, 1975), central Atlantic (Leon and Malkov, 1979; Galaktionov, 1984; Sherstyukov and Nostov, 1986; Kotlyar, 1987), Indian (Ivanin, 1987) and Pacific oceans (Humphreys *et al.*, 1984; Seki and Tagami, 1986; Horn and Massey, 1989; Massey and Horn, 1990). Most of the information that is available about the biology of *B. splendens* has come from fisheries sources and consists mainly of length frequency catch curves taken at different times from different places, as well as age frequencies and length-at-age curves.

Age estimates for *Beryx splendens* have been made from otoliths (Ikenouye, 1969; Leon and Malkov, 1979; Kotlyar, 1987; Massey and Horn, 1990), using various interpretations of what are annual opaque zones. Although there have been a number of studies depicting opaque zones in the otoliths of *Beryx splendens,* they have been vague as to the variation in width and distribution of such bands. In the description by Ikenouye (1969) opaque bands were illustrated in a drawing. The same drawing was reproduced by Leon and Malkov (1979) even though it was (from its shape) evidently from a small fish. Similarly, Massey and Horn (1990) illustrated the otolith of *B. splendens* with a drawing of an otolith from a small fish. In some interpretations more than one opaque zone is laid down each year, and in others only one opaque zone is laid down each year. The more than one zone per year interpretation of Ikenouye (1969) is supported by growth rates observed from tagging (Ikenouye and Masuzawa, 1967). Other interpretations of only one zone per year have been based on the observed annual cycle of opaque and hyaline zones in the catch, i.e., the method of marginal increments (Horn and Massey, 1989; Massey and Horn, 1990) or simply asserted (Kotlyar, 1987).

The sagittal otolith of most teleosts contains microincrements usually > 1 µm width of the type that have been shown to be deposited daily over certain periods (at least) in the adult lives of many fishes (Panella, 1971; Ralston and Miyamoto, 1983; Laurs *et al.*, 1985; Wild, 1986; Gauldie, 1991; Pulfrich and Griffiths, 1988; Smith and Kostlan, 1991) as well as most of the lives of physiologically unperturbed juvenile fishes (Campana and Nielson, 1985; Jones, 1985), although the otoliths of some species may have a complex crystallinity that may obscure microincrement growth (Davies *et al.*, 1988). Continuous microincrement growth results in the possibility of rapid and inexpensive age estimation from the simple process of dividing the length of the otolith growth axis by average microincrement width (Ralston, 1985; Ralston and Williams, 1988; Gauldie *et al.*, 1989; Smith and Kostlan, 1991). In their study of otolith-based ageing methods for *Beryx splendens* Massey and Horn (1990) describe the use of microincrements in one otolith to estimate age, but they emphasize that a comprehensive daily growth ring analysis of age was not attempted in their paper.

The continuity of microincrement deposition is essential to the use of average microincrement widths in estimating age. Continuity of microincrement deposition also implies that the otolith contains in its crystal structure a continuous record of the sequence of those events in the life of the fish that cause physiological effects which are recorded in the chemistry of the otolith. Microscopic analysis of the crystalline structure of otoliths of *Macruronus novaezelandiae* has shown (Gauldie, 1993) that episodes of microcrystalline growth occurred that were of the form expected from chemical models of re-nucleation episodes (Gauldie *et al.*, 1991) that would follow pauses in otolith growth. In the otolith of *M. novaezelandiae*, the continuous growth of microincrements around such pauses in otolith growth offered a means of estimating errors in age estimates based on average microincrement width. This study describes the microincrement structure of the otolith of *B. splendens* and compares the microincrement-based interpretation of age with the age assigned by Ikenouye (1969) and Massey and Horn (1990). This study examines sources of error in age estimation errors based on microincrements, and compares ages estimated from the opaque zone patterns that are commonly observed in the otolith of *Beryx splendens* with ages estimated from microincrement width.

MATERIALS AND METHODS

This study is restricted to the sagitta of *Beryx splendens,* which is referred to as the otolith in the text. Otoliths were extracted from a sub-sample of individuals taken more-or-less randomly from the catch. Catches were made at two stations off the East Coast of the North Island of New Zealand: The Palliser Bank (total 198; 101 males, 97 females) and the Tuaheni Bank (total 220; 108 males, 112 females) in November 1985. Otoliths were collected into paper envelopes and stored dry until analyzed.

A set of ten otoliths was mounted whole on pin-stubs with epoxy resin, sputter-coated with gold, and photographed with a Philips 505 SEM. These otoliths were then broken by finger pressure, remounted, re-coated and photographed with a Philips 505 SEM. Images of whole otoliths and broken sections were recovered from this group of otoliths.

A second set of otoliths was used for microincrement analysis. Otoliths were mounted on glass slides with epoxy resin and ground down horizontally to the plane of the dorsal growth axis that contains the microincrement series. Otoliths were removed by softening the epoxy resin with alcohol and were re-mounted on pin stubs. The ground surfaces were generally etched for 30 s (30 min. for prolonged exposures) in 0.1 M ethylene diaminotetracetic acid (EDTA) solution at pH 2.5-3.0. The etched surfaces were dried, sputter-coated with gold, and photographed for microincrements and checks using the Philips 505 SEM. Both the recognition and measurement of microincrements are essential to the use of microincrements both in estimating age and calibrating biological events in the life of the fish (Campana and Neilson, 1985). Recognition of microincrements requires a clear distinction to be made between microincrements and the crystalline lamellae of the otolith that show a pattern of etched marks analogous to that of microincrements (Gauldie *et al.*, 1992). The lamellae problem can be avoided by high magnification studies of etched otoliths that show the characteristic morphology of microincrement as parallel crystallites stacked orthogonally to the organic layer of the microincrement (Gauldie and Nelson, 1988). While this approach is only a rule-of-thumb, it is based on demonstrable morphological characters.

A third set of 18 otoliths was taken from the Palliser Bank sample and consisted of a stratified sample of 3 otoliths (randomly mixed males and females) from each 5 cm size class 20-25, 25-30, 30-35, 35-40, 40-50 cm with three additional otoliths from the 35-40 cm group. Sex and length were recorded for each otolith. This set was used for estimation of average microincrement width. Otoliths were photographed whole from the anti-sulcal side with a WILD stereo microscope, then mounted in epoxy resin on glass slides, ground and polished to allow the microincrement series in the longest dorsal prism of the otolith (the growth axis) to be read in an optical microscope. Microincrement width was measured as the average of twenty consecutive microincrements at intervals chosen at random along the growth axis of the otolith. In the smallest otoliths 5 intervals were used and in the largest otoliths up to 12 intervals were used. In the eighteen otoliths examined 80 observations of the average of twenty microincrements each were obtained.

The ultimate zone at the edge of the otolith forms the margin upon which the marginal growth increment method of age validation is based. The application of this well-known method to the otoliths of *Beryx splendens* has been described in Massey and Horn (1990). Essentially, the width of the margin is assumed to reflect the stage in the annual cycle of growth that the fish was at when it was caught. The width of the margin reflects the width of the zone that it is to form, and therefore the margin type assigned to the fish and the thickness of the otolith are correlated. Margin types are scored as: type 1, *no margin*; type 2, *very fine margin*; type 3, *fine margin*; type 4, *narrow margin*; type 5, *medium margin*; and, type 6, *wide margin* (following the methods described in Massey and Horn (1990)).

Otolith "opaque zones" of the Palliser Bank and Tuaheni Bank samples were read by reflected light under oil at 10x magnifications as described by Massey and Horn (1990). The illustration of "opaque zones" of Massey and Horn (1990) is terse, but generally there was good agreement between my results and length-at-age curves published by Massey and Horn (1990) although I cannot be sure that I was using exactly their method of scoring. The otolith samples used to read "opaque zones" were drawn from both the Palliser Bank and Tuaheni Bank samples as stratified samples representative of size groups. The sample sizes are given in the text. The growth axis of the dorsal prism (line in Fig.1a) of the otolith of *Beryx splendens* is recurved (Fig. 1a) making direct measurement of prism length difficult, particularly for large samples. However, a subset of ten otoliths showed that the correlation between the arc of the true growth axis (dotted line in Fig. 1a) and the chord between the nucleus and the end of dorsal prism was greater than $r^2 = 0.99$. Consequently the chords between the nucleus and the dorsal edge of the longest prisms were measured directly and converted to true axial length of the prism.

The thickness of the otolith refers to the width of the otolith in the anti-sulcal to sulcal plane. Thickness was measured using vernier calipers accurate to $\pm$ 0.025 mm.

As more and more new otolith data accumulate, perception of the interrelationships between various parts of the otolith changes and, inevitably, so does nomenclature. Most of the specialized terms used are either well-known or are available in Gauldie *et al.* (1991). The significant departure from standard nomenclature are the avoidance of the term annulus for the same reasons set out for scales in Gauldie *et al.* (1990), and specific use of the terms prism, nucleus and primordium. The term prism is widely used in the molluscan literature to describe the integral growth units of molluscan shells. The application of the term to the analagous structures in fish otoliths are described in Gauldie (1993). The terms prism, and prismatic growth, have been used to describe crystal growth in otoliths at a lower level of organization than the more general usage (e.g., Morales-Nin, 1986; 1987). The definition of nucleation by Mutaftshiev (1989) is "The name nucleation designates the emsemble of processes leading to the formation of a new, stable, phase inside an unstable mother phase." The chemical definition implies that the original point of growth

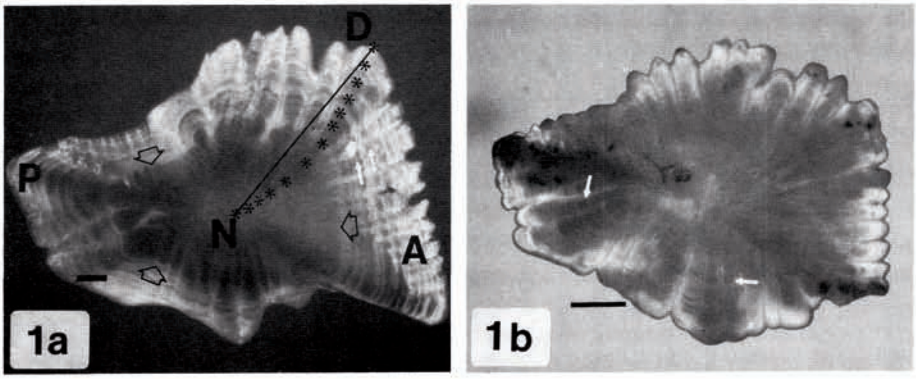


Fig. 1. - a. The sagitta otolith of an adult *Beryx splendens* viewed from the anti-sulcal surface by transmitted light shows longer curving prismatic growth in the anterior (A) dorsal (D) part than in the ventral area. Zonation is most readily visible in the anterior and dorsal part of the otolith, less clearly along the posterior rostrum (P) and much of the ventral segment. The arc corresponding to the longest nucleus-to-dorsal prism is picked out with stars and the chord corresponding to the shortest distance from the nucleus (N) to the dorsal edge of the prism is shown as a straight line. The boundaries of the inner dark zone are shown by open arrows. Bar = 1 mm. b. The sagitta otolith of a juvenile *Beryx splendens* viewed from the anti-sulcal side shows the same darker appearance and similar outline to the central part of the adult otolith. Narrow opaque zones (arrows) appear within the darker central part of the otolith. Bar = 1 mm.

is appropriately called the nucleus. Definitions of microincrement, check and zone are as follows:

Microincrement is an abbreviation for daily microincrement that consists of a broad crystalline deposit with a low matrix content coupled with a narrow matrix deposit of low crystal content. In optical sections, microincrements are recognised by the alternating light and dark sections caused by changes in refraction due to the matrix content. In etched sections, microincrements are recognised by alternating less-etched, broad, mineral-rich section coupled with a more-etched, narrow, matrix-rich section.

Checks are discontinuities in otolith growth that usually result in changes in phase in otolith material deposited on either side of the discontiuity. Occassionally checks appear without such changes in phase and cannot be distinguished from microincrements with greater than normal matrix content. Checks recognised as changes in refraction in optical sections may not correspond to checks recognised by differences in degree of dissolution in etched sections.

Zones are optical discontinuities that have the appearance of a dark band with diffuse edges. Zones can be generated by refraction around both surface and internal discontinuities in crystal structure of the otolith, as well as broader scale changes in otolith chemistry that cause changes in the refractive index of the otolith material (e.g., Gauldie, 1987; 1988).

RESULTS

Gross morphology

The whole otolith of an adult (41 cm fork length male) *Beryx splendens* had a dorsal growth segment composed of a group of prisms curving dorsally and anteriorly from the nucleus (Fig. 1a). The anterior segment typically had a large number of dorsal prisms with many major and minor opaque zones (observed by transmitted light) running from the ventral margin around the dorsal growth axis, fading out in the restricted growth area of the posterior ventral part of the otolith (Fig. 1a). The ventral part of the otolith was composed of a fewer number of shorter prisms than those in the dorsal part of the otolith (Fig. 1a).

Opaque and hyaline zones

The otolith of *Beryx splendens* had a complex opaque banding structure when observed by either transmitted or reflected light. This complexity resulted in increasing numbers of zones or bands with increasing magnification. None of this complexity is illustrated in either Ikenouye (1969) or Massey and Horn (1990). Furthermore, the summarizing effects of low magnification observation under oil of the opaque zone structure of the otolith provide a misleadingly simplified view of what proved to be a complex structure.

The central part of the adult otolith had a dark (by transmitted light) central region (Fig. 1a) which comprised the whole otolith in a smaller (21 cm fork length male) *Beryx splendens* (Fig. 1b) and can be regarded as the first broad opaque zone, even though there were evidently minor opaque zones within this broad zone (Fig. 1). This central dark zone is evidently the "nucleus" depicted by Massey and Horn (1990). The relationship of the central dark zone to the rest of the otolith can be evaluated in terms of the radius of the nucleus-to-dorsal axis of the otolith. The nucleus-to-dorsal axis of the otolith of most species is particularly important in fish ageing studies. Increasing otolith size often results in the ventral edge of otolith resting on the bony floor of the otic capsule (Gauldie and Nelson, 1990; Smith, 1991). In most fishes, including *B. splendens,* the least restricted path of growth is towards the dorsal exit of the otic capsule that corresponds to the nucleus-to-dorsal axis of the otolith.

Measurements of the radius of the nucleus-to-dorsal axis for the whole otolith, and measurements of the radius of the nucleus-to-dorsal axis to the edge of the central dark region only, were both plotted against fish length for 45 whole otoliths that were more or less randomly subsampled from the Palliser Bank sample in figure. 2. The radius of the nucleus-to-dorsal axis of the whole otolith was fitted to fish length with a straight line (the correlation coefficient was high, $r^2 = 0.86$; and the regression was also statistically significant, $p > 0.01$). The radius corresponding to the nucleus-to-dorsal axis of the central dark region only was also fitted to fish length (there was no significant regression); both regressions were plotted to show their point of intersection (Fig. 2).

The dorsal part of the otolith typically showed a number of opaque zones (Fig. 1) by transmitted light. At low magnifications the opaque zones appeared to form discrete parallel bands, but at higher magnifications these bands were composed of groups of varying numbers of more narrow opaque zones. A sub-sample of 20 otoliths from 29 to 47 cm fork length (male and female) fish taken more-or-less randomly from the Palliser Bank sample were examined by transmitted light and the average width of opaque zones at low magnification (6.5x) was calculated by measuring back from the dorsal edge of the dorsal prism to the central dark part of the otolith past which no more opaque zones were counted. The same sample was then examined at higher magnification (26x) and the widths of opaque zones visible at that magnification were measured. At low magnifications the average distance between the opaque zones that appeared as parallel opaque zones was 529 μm. At higher magnifications more narrow opaque zones could be detected, both as groups comprising the lower magnification opaque zones, and as single zones lying between such

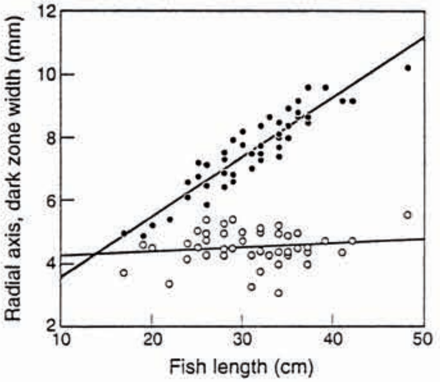


Fig. 2. - The radius (mm) of the inner dark zone (open circles) of the otolith of *Beryx splendens* and the total radius (mm) of the dorsal prism (closed circles) are plotted against fish length (cm).

opaque zones. The narrow opaque zones had an average width of 94 µm. The wide opaque zones correspond to the "opaque zones" and the narrow opaque zones may correspond to the "check rings" of Massey and Horn (1990) although it is difficult to draw comparisons with their diagrammatic drawing.

Marginal opaque zone analysis

The thickness of the otolith (distance from sulcal to antisulcal side measured at the edge of the longest dorsal prism) increased with increasing size. There was a significant regression ($p > 0.01$) of wide, low magnification opaque zone width on otolith thickness. The regression indicates a tendency to read low magnification opaque zones as wider on larger (and therefore older) otoliths (Fig. 3a). The width of the narrow, higher-magnification, opaque zones also showed a significant regression ($p > 0.01$) on otolith thickness with less evident variability (Fig. 3a). Opaque zones can be used to test age estimation following the method of marginal increment width. Following the methods of Massey and Horn (1990), it was possible to plot margin type against age frequency determined by the "opaque zone" method of Massey and Horn (1990) (Figs. 3b,c). Rotating the margin type against age frequency plots (Figs. 3b,c) showed that wider marginal types appeared more commonly in older fishes, and that both narrow and wide marginal types appeared in both older and younger fishes.

Crystalline structure

SEM examination of outer surfaces and sections

SEM studies of the otoliths surface of *Beryx splendens* showed a pattern of sculptured lines (Fig. 4a) that averaged 88 µm width. These sculptured lines corresponded to the narrow, 94 µm width, opaque zones observed at 26x magnification. Broken sections of some otoliths showed that some of the formations that cause surface sculpturing persisted inside parts of the otolith as insertions from the surface (Fig. 4a). Patches of the exposed surface of such insertions within the otolith (Fig. 4a) had a similar surface appearance to that of the surface sculpturing. The pattern of sculptured lines on the surface of the otolith started at approximately the margin of the central dark part of the otolith which has the form of a step, with a marked transition in the crystalline texture of the surface of the otolith (Fig. 4b). The surface crystal at the margin, and over the central part of the otolith, was very coarse (Fig. 4b). The otolith surface in figure 4b showed evidence of a natural

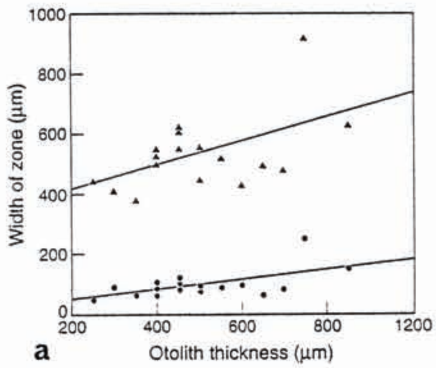
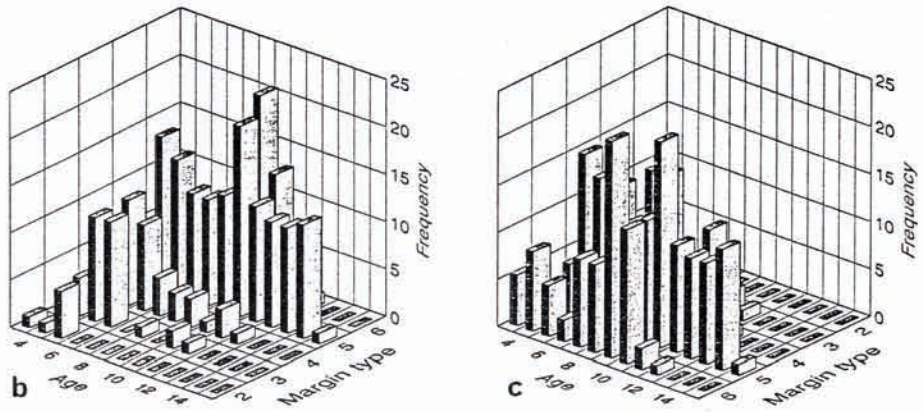


Fig. 3. - a. The widths of the low magnification zones (diamonds) and the widths of the narrow zones (closed circles) are plotted against the thickness of the otolith *Beryx splendens*. b,c. Frequencies of age in years (from opaque zones) and marginal type (from Massey and Horn, 1990) are shown rotated throughly 180° (b to c) to illustrate more clearly the age/ marginal type dependence for a sample drawn more-or-less at random from both the Palliser and Tuaheni Bank samples.



circular deposition pit on the surface. In some otoliths such deposition pits are more well developed and appear over most of the area of the central dark part of the otolith.

Spalling lines (Gauldie *et al.*, 1991) also occurred in broken sections of the otoliths of *Beryx splendens* (Fig. 4c). The fine crystal layer that gives the spalling line its characteristic appearance was about 10 µm wide. Spalling lines occurred in the medial growth axis of the otolith, which was sharply discriminated from the crystals of the radial axes that grow almost at right angles to the medial growth axis (Fig. 4c). This abrupt shift in direction of crystal reflects the flatness of the otolith of *B. splendens* whose thickness at its widest part was between 10 and 15% of the length of the nucleus to dorsal growth axis.

One of the predictions of the model of otolith growth of Gauldie and Nelson (1990) was that crystal size should follow the decreasing size gradient from the sulcus to the edge of the otolith that is predicted by the Gay-Lussac law for crystallization along pH gradients. The crystals of the sulcal surface were generally large, even near the dorsal edge of the otolith, becoming progressively larger along the sulcal side of the otolith and reaching their greatest diameter in the crystals observed on the sides and apex of the sulcus groove of whole otoliths (Fig. 5). The crystals of both the sides and apex of the sulcus were evidently in the form of pseudo-mimetic hexagonal twins. The average diameter of crystals at the dorsal edge was 5.6 µm (s.d. = 0.6, based on measurements of 160 crystals from 3 otoliths); at a point mid-way along the sulcul side of the otolith the average diameter was 6.5 µm (s.d. = 2.7, based on measurements of 180 crystals from 3 otoliths); at the sulcus itself the

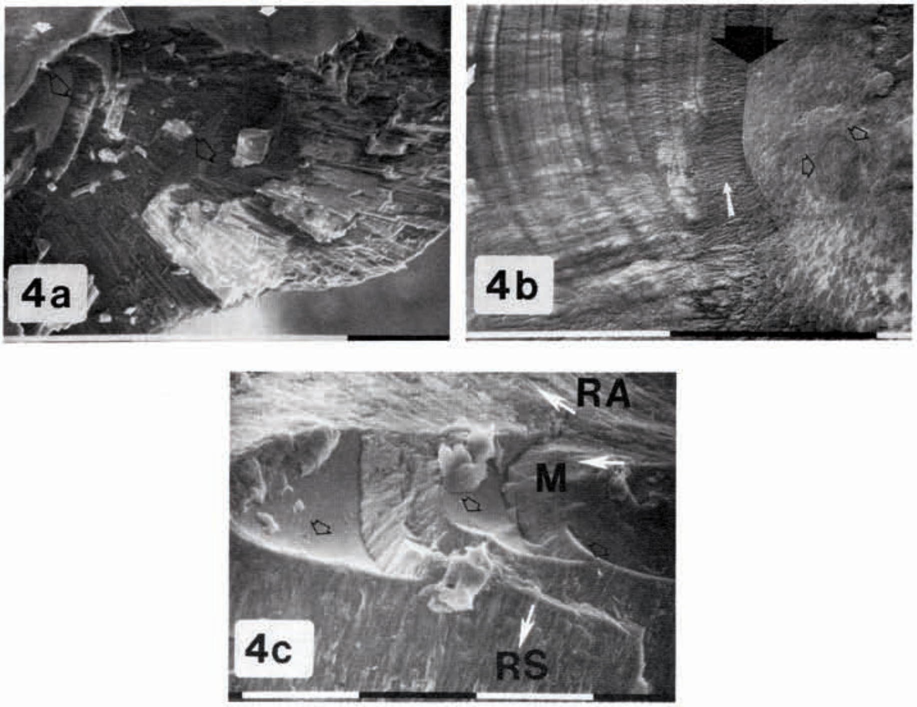
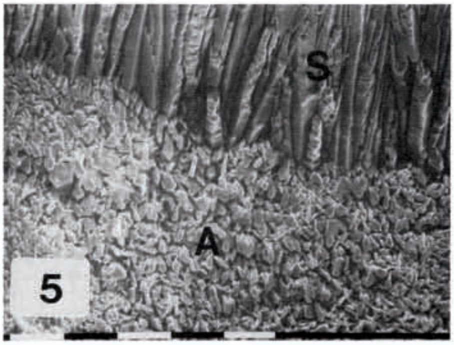


Fig. 4. - a. A broken section of the dorsal axis of the otolith of *Beryx splendens* showed surface sculpturing (white arrows) and internal spalling lines (open arrows) that are in some places associated with surface sculpturing. Bar = 1 mm. b. The edge central dark zone of the otolith corresponds to a major boundary (alack arrow) on the anti-sulcal surface of the otolith that marks the transition from an amorphous crystal surface with traces of etch-pit-like (open arrow) through a coarsely crystalline area (long white arrow) that marks the beginning of the sculptured surface of the otolith. Bar = 1 mm. c. Spalling lines (arrows) occur as fine-grained surfaces along the central growth axis of the prism. Most spalling lines only partially intersect the central growth axis. The radial crystals growing in the sulcal direction (arrow RS) diverge more abruptly from the medial crystals (arrow M) than do the radial antisulcal (arrow RA) crystals. Bar = 0.1 mm.

average diameter of crystals in the wall of the sulcus was 19.4 µm (s.d. = 1.4, based on measurements of 30 crystals) and the average diameter of crystals in the apex of the sulcus was 12.5 µm (s.d. = 2.4, based on measurements of 40 crystals).

Microincrements

Etched horizontal sections through the nucleus of the otolith of *Beryx splendens* showed a single nucleus surrounded by widening increments (Fig. 6). There was no primordium around the nucleus corresponding to that observed in some other species (e.g., Gauldie, 1993). Microincrements in sections near the nucleus (Fig. 7a) of the otolith were very wide compared to the rest of the otolith (average width in figure 7a of microincrements was 13.6 µm). Wide microincrements have been described as occurring both near the nucleus of the otolith (Gartner, 1991; Secor and Dean, 1992) and at some distance from the nucleus of the otolith of *Theragra chalcogramma* (Nishimura and Yamada, 1988). In



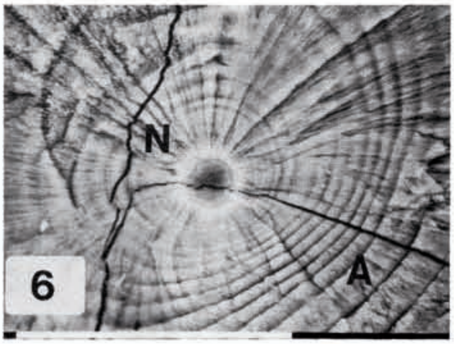


Fig. 5. - The crystals of the side (S) and apex (A) of the sulcus of the otolith of *Beryx splendens* were in the aragonite twinned form in both the side and apex of the sulcus, but with greater growth in the long axis in the crystals of the side of the sulcus. Bar = 0.1 mm.

Fig. 6. - The nucleus of the otolith of *Beryx splendens* has a well defined nucleus (N) with widening microincrements growing away from the nucleus. The antisulcal side (A) is to the lower right. Bar = 0.1 mm.

part, the width of microincrements has been increased by the angle of the section. In figure 7a it can be seen that the crystals of the microincrement point upwards to the viewer rather than laying flat. However, even if the angle of section is corrected for 30° of tilt in respect to the plane of the microincrement, the width would still be about 11.8 µm. Increasing the angle of section also tends to blur the boundary between the mineral and organic layers of the microincrement, decreasing the overall resolution of the microincrement itself, as can be seen in figure 7a. Occasionally, microincrements near the nucleus showed a tendency to form an unusual type of microincrement that had recessed central bands (Fig. 7b). Such microincrements could be interpreted as being either one or two microincrements depending on the interpretation of the central band. However, microincrements of this type occurred in sequences of between 10 and 30, and only in one part of the otolith, so that their

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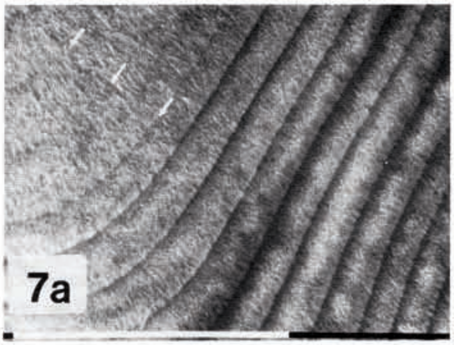
Fig. 7. - a. Microincrements close to the nucleus are very wide with crystals progressively tilting towards the observer and finally resulting in loss of legibility (arrows) towards the nucleus which is in the upper left hand direction. Bar = 0.1 mm. b. Some microincrements have flattened central bands (small arrows) lying between what appears to be proper microincrement boundary zones. Bar = 0.1 mm. c. Microincrements appear to be formed from stacks of crystals separated by narrow bands of etch-sensitive material (arrows). Changes in crystal direction (white arrows) are reflected in changes in the microincrement "front". Compression zones (C) result on local censoring of the true number of growing microincrements. Bar = 10 µm. d. As microincrement width decreases relative to crystal size incomplete etching results in crystals with a markedly "waisted" appearance (small arrows) that remain as intact crystallites across many microincrement layers. Bar = 10 µm. e. Microincrement legibility decreases towards the edge of the otolith where crystal width and microincrement width are of similar dimensions. Bar = 0.1 mm f. The width of microincrement changes in the plane of section (arrows), sometimes in association with a change in orientation of the underlying crystal that results in a loss of legibility (open arrows) as crystals become more perpendicular to the plane of the section. Bar = 0.1 mm. g. Optical sections showed microincrements (arrows) as well as the crystals (long arrows) structure of the otolith. Bar = 10 µm.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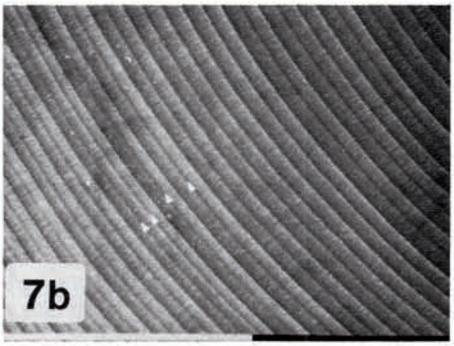
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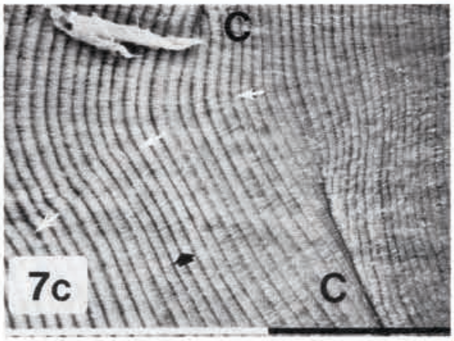
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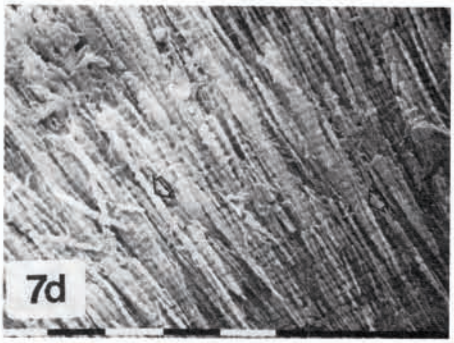
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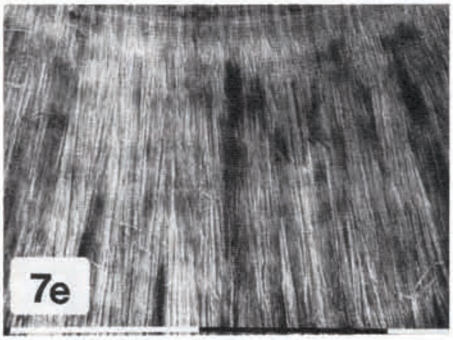
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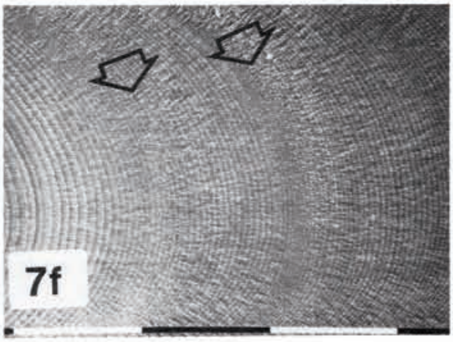
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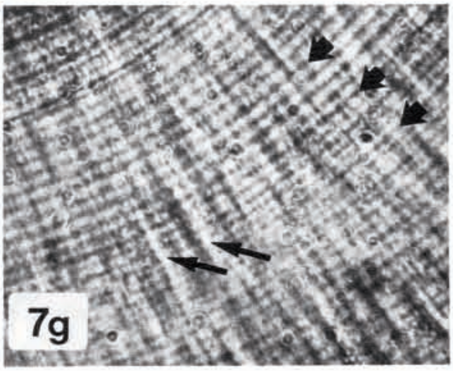
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effects on ageing errors is not significant. The difference between interpretation of one or two microincrements would cause a change in estimated age of 20 to 40 days and have no significant statistical effect on estimates of microincrement width. Similar structures have been observed in tuna otoliths (Wild, 1986).

Apart from the loss of legibility due to changes in the angle of crystalline growth close to the nucleus, the flattened shape of most of the otolith of *Beryx splendens* has the advantage of allowing microincrements to be followed from the nucleus to the dorsal edge of the otolith in single horizontal sections of the otolith. Microincrements of the otolith of *B. splendens* had the typical teleost morphology, being composed of parallel stacks of crystals lying more-or-less at right angles to narrow bands of organic material that were sensitive to EDTA etching (Fig. 7c) similar to those described in other species (Gauldie and Nelson, 1988). As a consequence of the orthogonality of the microincrement crystals to the organic boundary of the microincrement, any change in the direction of crystal growth is reflected in a shift in the direction of the microincrement "front" (Fig. 7c). The microincrement series in figure 7c also shows the censoring effect of compression zones in which microincrements are partially lost, even though the microincrement "front" continues to grow around such zones. In places, crystals (Fig. 7d) cross the narrow etch-sensitive zone of the microincrement and have a "waisted" appearance due to incomplete etching of the crystal. This was an important observation as it indicated that crystalline growth was continuous and that microincrements were inserted into the continuously growing crystal by a mechanism independent of the mineral growth phase of the otolith. Microincrements decreased in width towards the edge of the otolith with progressively greater interference in microincrement legibility as microincrement width became similar to crystal size (Fig. 7d). Crystal size shows very little change along most of the dorsal growth axis, going from an average width of 1.08 µm in the central part of the otolith to an average of 1.07 µm at the edge of the otolith. The crystals in figure 7e also showed a tendency to persist through a number of microincrements. In figure 7c there were also many crystals that either show some penetration of the etch sensitive layer, or show alignment of crystals on either side of the etch sensitive layer that suggested continuity of crystalline growth even in the central part of the otolith. Crystal orientation also affected both microincrement width and legibility as in figure 7f. Optical sections showed that without etching it was possible to observe microincrements of similar width and morphology as those observed in etched sections (Fig. 7g). The usefulness in age estimation of both microincrement numbers and their patterns of deposition depends on their legibility and on the continuity of their growth. The longest dorsal prism of the otolith of *Beryx splendens* contained a continuous sequence of microincrements from the nucleus to the dorsal margin. The following results show that microincrements could be counted right to the edge of the dorsal prism of the otolith even in the largest otoliths available for this study.

Growth interruption

Interruptions in the continuity of growth of microincrements were characterized by different kinds of crystalline ultrastructure. The first kind of ultrastructure had the appearance of a local interruption of otolith growth with continuing microincrement growth at the side of the interruption (Fig. 7c). Local interruptions of this kind sometimes resulted in a change in the direction of the main crystal axis resulting in a change in orientation of microincrement growth (Fig. 7c). More severe effects occur in some parts of the otolith with growth interruptions that extend further across the growth axis of the prism (Fig. 8). However, even in these severe disruptions there is still evidence of continuing microincrement

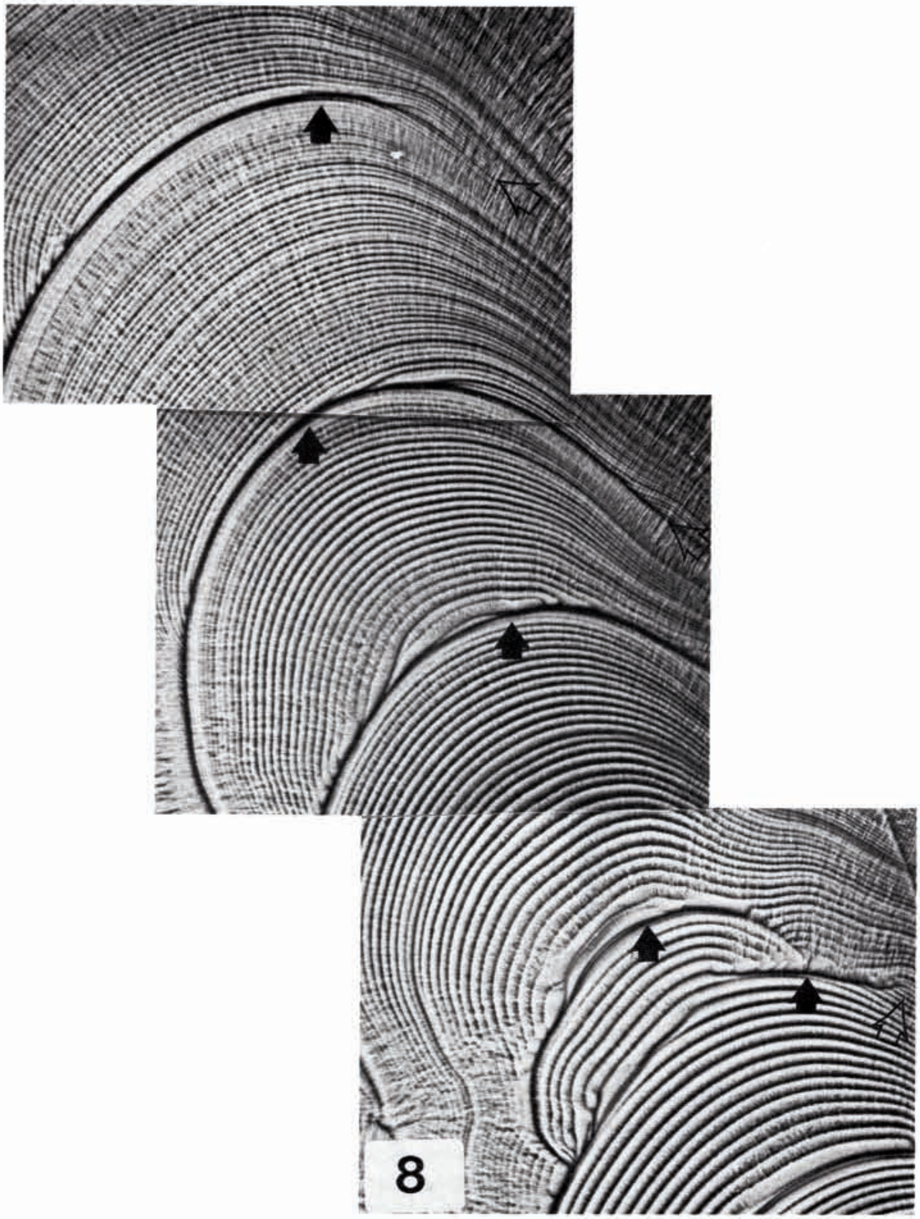

Fig. 8. - Growth disruptions in the otolith of *Beryx splendens* that severely deform the patterns of microincrement growth in the central part of the dorsal prism (arrows) are accompanied by continuing microincrement growth (open arrows) closer to the prism boundary. Bar = 0.1 mm.

deposition growing around the interruption (Fig. 8), until they meet the discontinuity at the edge of the prism (Fig. 8). Such severe disruptions affect the orientation of the main growth axis of the prism and result in an apparent loss of microincrements in counts estimated by dividing the length the central growth axis of the prism by the average microincrement width. However, the apparent loss of microincrements caused by under-counting at these disruptions was low. Fifteen disruptions in three otoliths showed an average loss of 4.8 microincrements (s.d. = 1.48) at each disruption, measured by comparing microincrement counts in the central axis against counts at the edge as in figure 8. The numbers of disruptions of this type in the dorsal prism ranged through 3, 5 and 7 in the 3 otoliths examined, resulting in a potential average loss of 14, 24 and 34 microincrement counts respectively. This kind of disruption always occurred in the more central part of the otolith that contained wider microincrements.

Another kind of disruption occurred in the more distal part of the dorsal prism. This kind of disruption had the appearance of an abrupt halt in crystal growth along a particular microincrement boundary. This disruption appeared to result from locally enhanced etch sensitivity. This could be seen clearly in figure 9a in which four check-like structures appeared after etching. Two of the check-like structures in figure 9a (numbered 1 and 3) were not growth interruptions, but local changes in etch sensitivity. In both of these check-like structures, crystals could be seen passing through from one side of the structure to the other. Of the remaining two check-like structures or disruptions in growth, the more central one numbered 2 in figure 9a showed less etch effect at the upper and lower boundaries than at the centre. In the less-etched parts of the section microincrements grew up to, and passed by, what appeared to be no more than a more emphasized microincrements. In the central part of the check-like structure marked 2 in figure 9a, microincrements grew progressively more narrow as they approached the deepest etch part of the structure. The last check-like structure marked 4 in figure 9a showed traces of narrowing microincrements at one end, with deeper etching at the other end. There were traces of crystal continuity across both of the more deeply etched structures 2 and 4 in figure 9a suggesting that, without etching, crystal growth would have appeared continuous. The narrowing of the increments in the etched structure resulted in a much shorter intra-microincrement crystal. For the section in figure 9a, average crystal width is about 1.1 µm while microincrement width reduces from 1.7 µm to 0.9 µm at the etched structure, increasing the surface area-to-volume ratio of the intra-microincrement crystal, (and, therefore, the rate of etch), by 22%. If there were even more narrow microincrements obscured within the deeply etched clefts, then their relative sensitivity to etching would have been greater still. The deeply etched clefts in figure 9a all had the common feature of progressively more etch from the left hand (nucleus) side and an abrupt cessation of the right hand (dorsal) side. The dorsal side was characterized by a wider increment. The effect of this kind of change in etch-sensitivity is to produce what at low magnification has the appearance of a check in growth, but at higher magnification appears as a change in etch-sensitivity of the microincrement (Fig. 9a,b,c). To test the effect of etching, some sections were subjected to prolonged (30 min.) etching. The microincrements of the otolith of *Beryx splendens* proved to be still recognizable even after exposure to prolonged etching that resulted in disintegration of the mineral layer into crystals (Fig. 9d).

The third kind of disruption occurred in vertical sections along the nucleus-to-dorsal axis of the otolith in the crystalline structure of the sulcal part of the otolith (Fig. 9e). These disruptions had the form of etched crack-like structures about 5-10 µm wide that terminate abruptly within the structure of the otolith (Fig. 9e). It could be seen that they

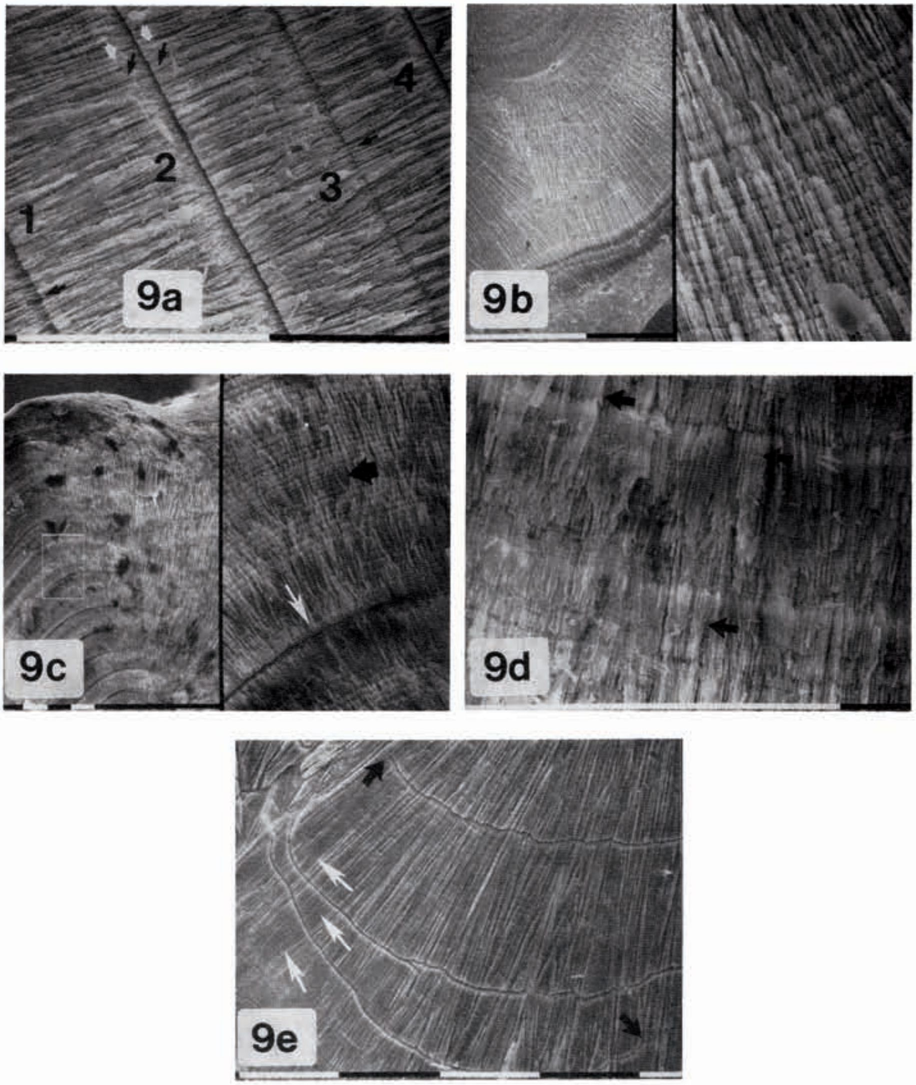

Fig. 9. - a. An etched section of the otolith of *Beryx splendens* shows four check-like structures (labelled 1-4). Structures 1 and 3 have continuous microincrement progression and in places (arrows) show crystals growing across the structure. Structure 2 shows a progressive deepening of the etch in the center. Microincrements (between white arrows) show a progressive decrease in width as they approach the deepest part of the etch. Structure 4 becomes progressively deeper from top to bottom. Traces (arrows) of crystal continuity can be seen in structures 2 and 4. Bar = 0.1 mm. b. Check-like structures visible at low magnification in etched sections of the otolith of *B. splendens* are from changes in etch sensitivity of microincrements (box; right hand frame). Bar = 0.5 mm. c. Check-like structures near the edge of the otolith (LHS box) at higher magnification appear as bands of more narrow microincrements (arrows) or discontinuities (white arrow) around which microincrement growth continues. Bar = 50 µm. d. Over-etching emphasizes the underlying crystal (arrows) but very even microincrement deposition patterns can still be detected. Bar = 100 µm. e. The crack-like discontinuities that appear in etched sections of the sulcal part of the otolith of *Beryx splendens* show abrupt terminations (arrows) and compressed microincrement sequences follow the contours of the discontinuity (white arrows). Crystals grow through the discontinuities in many places (open arrows). Bar = 100 µm.

were a part of the otolith structure and not preparation artefacts by the way that the microincrement-like structures in the sulcal part of the otolith showed compression (and censoring in the loss of such structures) that follows the line of the crack-like disruptions. Crystals show alignment on either side of the disruption, and in some cases, they appear to grow right through the disruption (Fig. 9e).

Age estimation by the method of average microincrement width

Microincrements were sufficiently legible to be measured from sections of otoliths observed by transmitted light. Microincrement width was taken as the average of twenty consecutive microincrement widths. The average microincrement width for each point was then plotted against distance along the nucleus-to-dorsal growth axis for all eighteen otoliths (Fig. 10). Below a distance of about 6 mm along the nucleus-to-dorsal growth axis, microincrement width was wide and variable, but past the 6 mm point, microincrement width was narrow and uniform. Comparison with figure 2 strongly suggests that the boundary of the inner dark zone of the otolith coincided with the point at which microincrements passed from wide and variable to narrow and uniform. The distance at which this boundary effect occurred did not vary very much between otoliths along the nucleus-to-dorsal growth so that an arbitrary cut-off point at a distance 5.9 mm along the growth axis could be used to divide the data set in figure 10 into two growth phases, one associated with the wide variable microincrements, the other associated with narrow, uniform microincrements.

Estimating age from the relationship between bi-phasic microincrement width and the length of the growth axis of the otolith requires one estimator for the inner, wide microincrements, and another estimator for the outer, narrow microincrements. These estimators were calculated from,

$$M_I = 17.319\text{-}2.6669d, \qquad d \leq 5.9, \qquad (1)$$

$$M_O = 2.7663\text{-}.1608d, \qquad 5.9 > d, \qquad (2)$$

where M_I is the width of the inner, wide microincrement, M_O is the width of the outer, narrow microincrement, and d is the distance along the dorsal growth axis. The scatter in microincrement width for estimator (1) was high, resulting in a low regression coefficient ($r^2 = 0.55$) although the regression was significant ($p > 0.01$). However, fitting alternatives, such as a logarithmic or a power function resulted in much lower regression coefficients. The scatter in microincrement width for estimater (2) was low, $r^2 = 0.93$. These estimators can be used to estimate biphasic average microincrement width, which can then be separately divided into the length of both the inner and outer parts of the otolith dorsal axis to give an estimate of fish age.

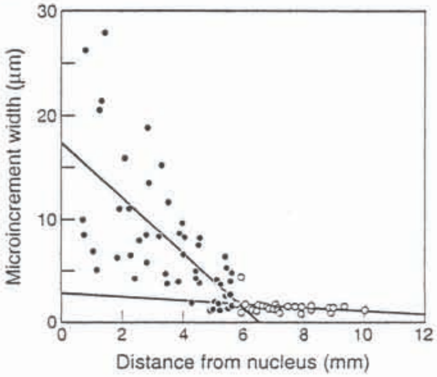

Fig. 10. - Microincrement width (mm) is plotted against distance (mm) from the nucleus along the nucleus-to-dorsal growth axis of the otolith of *Beryx splendens*. The figure is divided into two groups : The more widely scattered juvenile microincrement widths (closed circles) and the more tightly distributed adult microincrement widths (open circles). The juvenile and adult data are fitted with regression lines from equations (1) and (2) in the text respectively.

Length-at-age estimated by the microincrement method for the Palliser and Tuaheni samples are shown in figures 11a,b. The Palliser sample was also aged using the opaque zone method described by Massey and Horn (1990) and the results are shown in figure 11a. Comparison of length-at-age curves showed that the microincrement technique indicated growth rates about twice as fast as the annual zone method, i.e., two zones for each true annual increment. Both the opaque zone and microincrement methods showed a large scatter of points that may indicate heterogenity in growth rate, but there was no significant difference in growth rates between males and females.

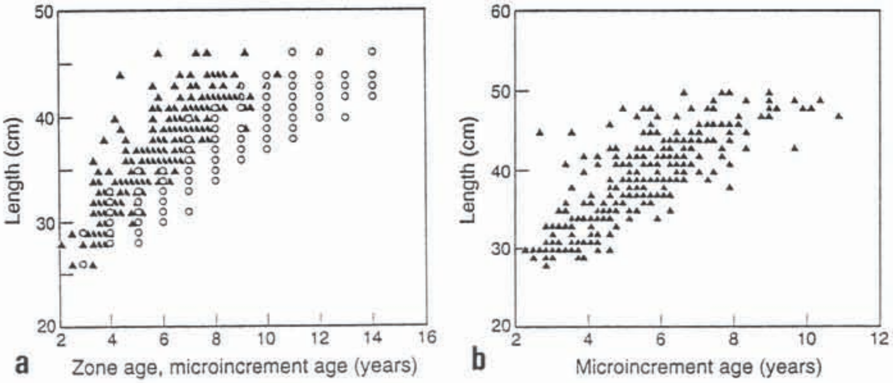

Fig. 11. - a. Length (cm) at age (years) curves are shown for *Beryx splendens* in which the zone method (open circles) and microincrement method (diamonds) results for the Palliser sample are plotted together. b. A length (cm) at age (years) curve based on the microincrement method is shown for the Tuaheni sample.

DISCUSSION

The kinds of questions that are asked of otoliths by fisheries biologists are nearly always related to those structures in the otolith whose periodicities are thought to be in some way related to the age of fish. To facilitate this approach I propose two basic anatomical models of otolith structure periodicities: the zone/check model and the microincrement model. In a concise form these are the models:

1. The zone/check model: In this model, opaque zones, (i.e., changes in optical density) occur in the otolith because the rate of otolith growth determines the ratio of mineral to matrix. Decrease in the rate of growth of the slow growth zone that is mineral-deplete (and matrix-rich) causes the width of the slow growth zone to become more and more narrow until it eventually appears as a very narrow zone, or check. This implies that non-annual stresses of the kind that can cause slow growth may result in a range of structures from zones to checks. In this model, mineral growth may be continuous only in the mineral phase of the zone, because the check phase of the zone implies a discontinuity in mineral growth. The use of this model in age estimation depends on the ability of the reader to distinguish between annual and non-annual checks.

2. The microincrement model: In this model microincrements are deposited continuously over the life of the individual along the dorsal growth axes (as well as other

axes). Variations in microincrement width lead to changes in optical density (and etch resistance) that lead to both zones and checks that may or may not be annual. Mineral growth is continuous. The use of this model in age estimation depends on mineral growth being continuous and that microincrements are inserted into the mineral phase by a clock-like mechanism with a period of one day.

The otolith of *Beryx splendens* has zones, checks and microincrements that have all been used to develop conflicting estimates of age. Which estimate is correct? The ideal method would be to compare observed growth (Δl) increments over time (Δt) increment, (i.e. Δl /Δt), with the growth increments (Δl) over age (Δa) increments expected from *a priori* models, (i.e. Δl/Δa). But for this method to work it is necessary to have a unique value of Δl/Δa for every Δa. This is an improbable condition. The alternative is a statistical reduction of the observed individual variation in Δl/Δt to a mean value to compare with some *a priori* mean value of Δl/Δa. A more practical approach would be to examine the support offered for different age interpretations and to score them as supportable or unsupportable. After all, every different age estimation technique in use must have at least one convincing supporting argument otherwise the technique in use would have never been developed. Scoring of interpretations of periodic structures in the otolith of *Beryx splendens* can be tested by using information from sources both external and internal to the otolith and a table of scores developed (Table I). Scores are +1 for positive support, 0 for neutral support, -1 for negative support, i.e., disagreement. For this paper, the age interpretations are either in terms of the zone/check model or the microincrement model.

Table I. - Scoring of interpretations of periodic structures in the otolith of *Beryx splendens*.

Model tests	Zone / check	Microincrement
Tagging experiments	0	+ 1
Length modes	0	0
Age marks	0	-
Marginal increments	0	+ 1

Testing by external arguments

Tagging experiments

Studies of tagged *Beryx splendens* by Ikenouye (1969) showed that 1) tagging did not affect apparent growth rate (Ikenouye and Masuzawa, 1967) and 2) two opaque zones were deposited each year: "the alfonsin is also proved to secure yearly two bands in otolith" (Ikenouye, 1969). Ikenouye's results agree very closely with the microincrement ageing technique which indicated two opaque zones per true annual growth increment. Tagging experiments are positive (+1) support for the microincrement model, and ambivalent (0) support for the zone check model.

Length modes

Inspection of Massey and Horn 's (1990) data set shows that the length frequency modes of *Beryx splendens* were unimodal and skewed to the right with one or two possible modes in the skewed part of the data. There was no evidence of either a modal progression of year classes or strong year classes by length that would allow the application of the

Peterson method (strong year classes) to age interpretation. However, examination of length modes from data sets that include juveniles described by Kotlyar (1987) and Galaktionov (1984) also apparently led those authors to the interpretation of two annual marks per year in populations separate from those studied by Ikenouye (1969). Length modes for different studies offer neutral (0) support for both the zone/check model and for the micro-increment model.

Testing by internal arguments

Age marks

The zones, or checks, used by Ikenouye (1969), Massey and Horn (1990), Kotlyar (1987), Galaktionov (1984) and Leon and Malkov (1979) were all observed by reflected light from the anti-sulcal surface of the whole otolith of *Beryx splendens*. Annual zones or checks are usually observed in broken or ground sections of otolith that have been burned to improve zone legibility (Bagenal, 1974). Such zones are internal, not external features of otoliths. Some species, such as flatfishes, have thin, flat, translucent otoliths through which the relatively few wide internal zones within the otolith can be successfully read externally by transmitted light. However, in *Beryx splendens* it is evident that "zones" are caused by surface sculpturing, as in *Hoplostethus atlanticus* (Gauldie, 1988). In other species with known ages surface sculpturing is not related to age, e.g., in the *Oncorhynchus tshawytscha* (Gauldie, 1991), and there is no direct evidence in the literature to support an annual interpretation of surface sculpturing of otoliths.

The widths of zones, or checks, of the whole otolith of *Beryx splendens* were also correlated to the thickness of the otolith. In addition, the widths of zones were related to the magnification employed in the observation of the otolith, so that low magnification observations effectively integrated many smaller zones or checks into the larger ones observed at low magnifications. Otolith thickness is related to age, and therefore the legibility of the zones used in age estimation must decrease with age. These kinds of artifacts seriously impair the usefulness of such zones in age estimation and must be regarded as at least ambivalent (o) support for the zone/check model.

Marginal increments

The marginal increment method of validating ages requires that the observed marginal increment must be independent of age. At the point of sampling, all otoliths should have more-or-less the same degree of marginal increment; otherwise different otoliths would acquire age marks at different rates, i.e., ageing would not be linearly time-dependent. The effect of otolith thickness on the width of the zone also applies to the width of the margin of the developing ultimate zone, the marginal increment. When the width of the margin is compared to assigned age in a sample of otoliths collected at the same time, it is evident that the width of the marginal increment is smallest in younger fishes and wider in older fishes. This is the reverse of what one would expect from the faster and slower growth rates expected from younger and older fishes respectively. Zone legibility, and therefore marginal increment legibility, decreases with otolith thickness, which would lead to wider marginal incremental width with increasing age. This kind of circularity impairs the marginal increment method of validation.

The primary validation of the one zone-per-year interpretation of Massey and Horn (1990) came from marginal increment series. The mean marginal increment indices of Massey and Horn (1990) are described as a "sudden drop in mean marginal index in June indicates that opaque material has started forming in June "that indicate one opaque and one hyaline zone are laid down annually". However, two of the mean marginal increment index graphics of Massey and Horn (1990) also showed a rise in mean marginal index from the January minimum that is followed a second maxima in November/December. Why should the January minimum not also be regarded as a second annual event leading to two opaque zones per year? In the absence of any physiological explanation of what an opaque zone may be, the mean marginal index data of Massey and Horn (1990) can be just as easily interpreted to indicate two opaque zones per year as one. Marginal increment arguments must be regarded as offering at best neutral support for the zone check model and positive support for the microincrement model.

The external structure of the otolith shows a crystalline boundary at the edge of the inner dark zone. This boundary marks a change from a more amorphous central region of the otolith to the sculptured surface of the adult otolith. The deposition pits and coarse crystallinity are indicative of rapid crystallization. The dark zone extends to a point on the dorsal prism that corresponds to the point of inflection between the wide variable microincrements and the narrow uniform microincrements. The wide microincrements vary between about 4 μm and 29 μm in width with average width of about 9 μm estimated from the fitted line in figure 3, leading to an estimated average age of 22 months at the edge of the dark zone. Juveniles were described by Galaktionov (1984) as fish 19.6 cm average length, and he reported daily vertical migrations of 350-400 μm through temperatures of 8.3 to 15.5°C, reaching as high as the bottom of the thermocline. Adults were described by Galaktionov (1984) as staying within 200 m of the bottom. In other species otolith microincrement width is related to temperature (Gauldie, 1991) and it appears that the wide, variable microincrements of the fish less than 20 cm long reflects the more variable temperature environment of the juvenile phase. The narrow, uniform microincrements laid down in fish greater than 20 cm reflect the less variable temperature environment of the adult phase. Comparison of the length of the fish with the length of the growth axis of the otolith showed the edge of the dark zone to correspond to a length of about 20 cm, similar to the length of 19.6 cm assigned as the upper limit of juvenile length by Galaktionov (1984). Juvenile *Beryx* have a different appearance from to the adult fish (Abe, 1969; Abe and Maruyama, 1971; Krefft, 1976; Keene and Tighe, 1984; Mundy, 1990) to the extent that they have been described as a separate species to the adult (Roule, 1924). Although juveniles with characteristic filamentous dorsal fins have been described up to 26 cm total length, the upper bound of fork length for juveniles is about 20 cm. The apparent association between fish length, inner dark zone boundary and microincrement width inflection may reflect the completion of the metamorphosis from juvenile to adult. However, the otolith microincrement width data imply that the completion of the metamorphosis is size, not age, dependent and the microincrement counts leading to an age of 10 months for the "nucleus" of Massey and Horn (1990) fall within the expected range, as does the observation of Ikenouye (1969) that in some individuals the first annual mark is within the central dark zone of the otolith. Life history data provide positive support for the microincrement method, and neutral support for the zone/check model.

Examination of table I shows that the microincrement model is more strongly supported than the zone/check model of age estimations leading to the conclusion that two opaque zones are deposited each year in the otolith of *Beryx splendens* there by supporting the interpretation of Ikenouye (1969). A reasonable interpretation of otolith growth is that it is generally continuous and that ages based on microincrement width are better supported than those derived from interpreting the optical effects of the surface sculpturing of the otolith as annual marks. Nonetheless, other as yet unexplored internal checks may prove to be annual.

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